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Aggressiveness as a component of fighting ability in pigs (Sus scrofa) using a game-theoretical framework

Irene Camerlink[a, *], Simon P. Turner[a], Marianne Farish[a], Gareth Arnott[b]

[a]Animal Behaviour & Welfare, Animal and Veterinary Sciences Research Group, Scotland's Rural College (SRUC), Edinburgh, U.K.

[b]Institute for Global Food Security, School of Biological Sciences, Queen's University, Belfast, U.K.

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*Correspondence: I. Camerlink, Animal Behaviour & Welfare, Animal and Veterinary Sciences Research Group, Scotland's Rural College (SRUC), West Mains Road, Edinburgh EH9 3JG, U.K.,

E-mail address: Irene.Camerlink@sruc.ac.uk (I. Camerlink).

Understanding animal contests has benefited greatly from employing the concept of fighting ability, termed resource-holding potential (RHP), with body size/weight typically used as a proxy. However, victory does not always go to the larger/heavier contestant and the existing

RHP approach thereby fails to accurately predict contest outcome. Aggressiveness, typically studied as a personality trait, might explain part of this discrepancy. We investigated whether aggressiveness forms a component of RHP, examining effects on contest outcome, duration and phases, plus physiological measures of costs (lactate and glucose). Furthermore, using the correct theoretical framework, we provide the first study to investigate whether individuals gather and use information on aggressiveness as part of an assessment strategy. Pigs, *Sus scrofa*, were assessed for aggressiveness in resident–intruder tests whereby attack latency reflects aggressiveness. Contests were then staged between size-matched animals diverging in aggressiveness. Individuals with a short attack latency in the resident–intruder test almost always initiated the first bite and fight in the subsequent contest. However, aggressiveness had no direct effect on contest outcome, whereas bite initiation did lead to winning in contests without an escalated fight. This indirect effect suggests that aggressiveness is not a component of RHP, but rather reflects a signal of intent. Winner and loser aggressiveness did not affect contest duration or its separate phases, suggesting aggressiveness is not part of an assessment strategy. A greater asymmetry in aggressiveness prolonged contest duration and the duration of displaying, which is in a direction contrary to assessment models based on morphological traits. Blood lactate and glucose increased with contest duration and peaked during escalated fights, highlighting the utility of physiological measures as proxies for fight cost. Integrating personality traits into the study of contest behaviour, as illustrated here, will enhance our understanding of the subtleties of agonistic interactions.

Keywords. aggression, assessment, contest, personality, pig, resource-holding potential

The understanding of what determines the winner of animal contests has benefited greatly from employing the concept of fighting ability, termed resource-holding potential (RHP) (Parker, 1974). Victory tends to go to the larger or heavier contestant, who generally has a greater ability to inflict injury, and therefore body size or weight is often used as a proxy for RHP. However, it is not always the case that the larger contestant wins (e.g. Neat, Huntingford, & Beveridge, 1998a). Rather, a range of factors will determine the overall ability of an animal to win a fight. Existing studies have uncovered a number of RHP correlates, in a variety of animal species (Arnott & Elwood, 2009a), demonstrating that multiple traits influence fighting ability (e.g. Stuart-Fox, 2006). Despite this research effort, problems persist in predicting contest winners, highlighting limitations of the existing RHP approach. Relying on relatively consistent morphological traits to predict likelihood of contest success fails to reflect changes in RHP caused by contextual factors that vary more rapidly in time, such as fatigue and experience of recent wins or defeats (Elwood & Arnott, 2012; Hsu, Earley, & Wolf, 2006).

Empirical studies, across a range of species, have demonstrated consistent between-individual differences in aggressiveness, characterized by its repeatability over time and across situations (reviewed in Briffa, Sneddon, & Wilson, 2015). Aggression has been defined as overt behaviour that is intended to inflict physical damage to another (reviewed in Nelson & Trainor, 2007). In the context of animal contests, aggressiveness has recently been mentioned as the propensity of an individual to use agonistic behaviour that could include initiating a contest, escalating a contest and attacking an opponent (glossary of Briffa et al. 2015). Intuitively, one might predict that a more aggressive individual may be more likely to win against a less aggressive opponent. If so, aggressiveness would constitute an important determinant of RHP. However, the importance of integrating animal personality within existing contest theory has only recently been acknowledged (Briffa et al., 2015), with

aggressiveness generally having been overlooked. However, boldness has been studied in contest settings in sea anemones, with boldness being correlated with aggressiveness (Rudin & Briffa, 2012). Aggressiveness might account for part of the discrepancy with existing studies in which, contrary to expectations, the contestant with apparently superior RHP does not win. This gives rise to the need to examine whether aggressiveness, in terms of a consistent behavioural response, is a component of RHP determining the overall chances of victory in a contest. To date, only two studies have examined the effect of aggressiveness on contest outcome, with Wilson, Grimmer, and Rosenthal (2013) finding that agonistic behaviour during a contest predicts dominance during a feeding trial in sheepshead swordtail fish, *Xiphophorus birchmanni*, while McEvoy, While, Sinn, and Wapstra (2013) found no effect of aggressiveness, measured as a combined score of agonistic behaviour towards a species model, on contest outcome in a social lizard species, *Egernia whitii*. In light of these conflicting results there is clearly a need to better understand the role of aggressiveness in animal contests.

In addition to influencing fight outcome, correlates of RHP provide animals with a means to gather information about the fighting ability of the opponent. Fighting is energetically costly and also bears the risk of injury or death (e.g. Briffa & Elwood, 2005; Glass & Huntingford, 1988; Kelly & Godin, 2001). Selection should therefore favour individuals that make appropriate decisions based on assessment of the costs and benefits of fighting (Maynard-Smith & Parker, 1976; Parker, 1974; Parker & Rubenstein, 1981), although such assessment does not always occur (Elwood & Arnott 2012; Mesterton-Gibbons & Heap 2014). There are two classes of theoretical models of animal contests that differ in their assumptions about the information-gathering abilities of contestants (reviewed by Arnott & Elwood, 2009a; Elwood & Arnott, 2012). The first type, termed self-assessment, assumes that each contestant has knowledge of its own RHP, but gathers no information about the opponent (e.g. ‘war of

attrition without assessment', Mesterton-Gibbons, Marden, & Dugatkin, 1996; 'energetic war of attrition', Payne & Pagel, 1996, 1997; 'cumulative assessment model' (CAM), Payne 1998). In these models, two animals compete up to a particular threshold at which point one gives up. Opponents each accrue costs (e.g. energy expenditure and injury) in line with their individual RHP, meaning that the inferior opponent will typically reach its threshold sooner and give up. In CAM costs also accrue due to the actions of the opponent, with superior opponents being better at inflicting costs. The second type, termed mutual assessment (e.g. 'sequential assessment model', Enquist & Leimar, 1983), involves individuals gathering information concerning relative fighting ability, typically interpreted as gathering information about an opponent's RHP and comparing this against their own ability. This need not be a cognitively demanding task (see Elwood & Arnott, 2013; Fawcett & Mowles, 2013 for discussion of this topic), yet it can be difficult to discriminate from other forms of assessment (Briffa & Elwood 2009). Mutual assessment has the advantage that the weaker contestant can terminate the contest as soon as it perceives it is inferior to an opponent and likely to lose, thus minimizing fight costs for both itself and the winner. However, assessing an opponent may be difficult and costly, and basing decisions on individual thresholds (self-assessment) to determine the degree of escalation and contest winner may be a more economical option under certain circumstances (see Mesterton-Gibbons & Heap, 2014 for relative costs of mutual and self-assessment). This may account for mounting recent empirical evidence of self-assessment (e.g. Brandt & Swallow, 2009; Copeland, Levay, Sivaraman, Beebe-Fugloni, & Earley, 2011; Rudin & Briffa, 2011; Tanner & Jackson, 2011; Martinez-Cotrina, Bohorquez-Alonso, & Molina-Borja, 2014; Tsai, Barrows, & Weiss, 2014).

Since the publication of a review paper that provided a framework to accurately discriminate between alternative assessment strategies (Arnott & Elwood, 2009a), there have been a number of empirical papers in a range of species examining RHP assessment strategies (e.g.

121 Garcia et al., 2012; Jennings, Elwood, Carlin, Hayden, & Gammell, 2012; Kasumovic,
122 Mason, Andrade, & Elias, 2011; Lopes Junior & Cardoso Peixoto, 2013; McGinley, Prenter,
123 & Taylor, 2015; Painting & Holwell, 2014; Palaoro, Dalosto, Costa, & Santos, 2014;
124 Reichert & Gerhardt, 2011; Yasuda, Takeshita, & Wada, 2012). However, these studies have
125 focused on morphological traits related to RHP. None have considered the prospect that
126 behavioural asymmetries in aggressiveness between contestants could be subject to the same
127 assessment strategies as more traditional RHP measures. The aggressiveness displayed by an
128 opponent provides a source of socially acquired public information (sensu Dall, Giraldeau,
129 Olsson, McNamara, & Stephens, 2005) that may enable an animal to adjust its response (e.g.
130 Hyman & Hughes, 2006). Such information could be particularly valuable if it reveals honest
131 information regarding behavioural consistency, thereby predicting future behaviour. Previous
132 work suggested that animals may be capable of comparing their aggressiveness to that of an
133 opponent (pigs, *Sus scrofa*: Erhard, Mendl, & Ashley, 1997), but this was not studied in
134 dyadic contests, nor was the correct theoretical approach to discriminate between different
135 assessment strategies used (Arnott & Elwood, 2009a; Taylor & Elwood, 2003).

136 Here we outline a framework to examine whether aggressiveness is a component of RHP and
137 whether or not it forms a part of the assessment strategy (either self- or mutual assessment)
138 used in the decision-making process of contesting animals. To test for assessment we
139 examined the relationship between winner and loser aggressiveness and contest duration,
140 using the framework advocated to discriminate between assessment strategies when using
141 traditional RHP measures (Taylor & Elwood, 2003, reviewed in detail by Arnott & Elwood,
142 2009a). Furthermore, we also examined the duration of display phases and escalated fighting
143 to indicate whether the assessment strategy may switch from one contest phase to another
144 (e.g. Hsu, Lee, Chen, Yang, & Cheng, 2008). Pigs provide a useful model system to test the
145 outlined predictions. In commercial pig production, aggressive behaviour is a problem and

has therefore been researched for a number of decades, generating a vast amount of knowledge including the behavioural pattern occurring during contests (McGlone, 1985; Rushen & Pajor, 1987). The social structure of domestic pigs is based on a dominance hierarchy formed through aggressive interactions (Meese & Ewbank, 1972), making them an ideal study system to investigate the influence of aggressiveness. While there is considerable descriptive work on pig aggression, the information-gathering and decision-making processes used by pigs to resolve aggressive encounters are poorly understood. As such, theoretical models developed to study contests offer a useful framework to better understand aggressive encounters between unfamiliar pigs.

In this study we assayed individual differences in aggressiveness, using the established resident–intruder (RI) test (Erhard & Mendl, 1997), which provides a measure of aggressiveness that is consistent over time (D'Eath, 2004; Clark & D'Eath, 2013). The resultant measure of attack latency provides an unambiguous, quantifiable measure of aggression in a format that can be interpreted within an RHP framework. Contests were then staged between pigs that varied in their level of aggressiveness, while matched for other traditional measures of RHP (body weight, Rushen, 1987). We also examined the effects of aggressiveness on contest behaviour, including the duration of display phases and escalated fighting. This is important because studies that only focus on changes in outcome without considering changes in fight cost may fail to find an effect where one actually exists (Arnott & Elwood, 2007). In other words, manipulating aggressiveness may alter the behaviour of contestants in a fight but without being sufficiently influential to affect outcome. The traditional measure of contest cost, namely contest duration, has been criticized as providing only a poor proxy for actual fight cost (e.g. McGinley et al., 2015). Therefore, in addition to using measures of duration, we also quantified the physiological costs of fighting in terms of lactate accumulation and glucose levels as has previously been advocated (e.g. Prenter,

171 Elwood, & Taylor, 2006). Based on previous studies we expected that lactate and glucose
172 would increase along with the contest duration (Briffa & Sneddon, 2007), whereby the loser
173 would have higher lactate and lower glucose values than the winner (Briffa & Elwood, 2005;
174 Schuett & Grober, 2000). Our experimental approach also enabled us to employ the correct
175 framework (Arnott & Elwood, 2009a) to examine whether individuals gather and use
176 information on aggressiveness as part of the contest decision-making process. Using this set-
177 up we tested the prediction that if aggressiveness is a component of RHP, then the more
178 aggressive individual should win.

179

180 **METHODS**

181 *Ethical note*

182 This study was carried out in accordance with the recommendation in the European
183 Guidelines for accommodation and care of animals, UK Government DEFRA animal welfare
184 codes, and adhered to the ASAB/ABS guidelines. The work was approved by SRUC's
185 Animal Ethics Committee (no. ED AE 21-2014) and the UK Government Home Office
186 legislation (Project licence PPL60/4330) under the Animals Scientific Procedures Act 1986
187 and was conducted in constant collaboration with SRUC's veterinary surgeon. Contests were
188 ended immediately when a clear outcome of winner and loser was apparent, or otherwise
189 after 30 min if no clear outcome could be identified. Four contests were ended because of a
190 fear response or repeated mounting behaviour of one of the pigs. Ending the contest
191 prematurely prevented any injury other than skin lesions from bites.

192

193 *Animals and housing*

194 A total of 114 young male and female pigs (Large White×Landrace sow × American
195 Hampshire boar) were studied. They originated from 17 litter groups, which were born in
196 three batches at the SRUC pig research farm. They were raised in conventional farrowing
197 crates. Males were not castrated and the tail and teeth were kept intact. Piglets were weaned
198 from the sow when they were 4 weeks of age and were studied at 9 weeks of age. After
199 weaning they were kept in the same litter groups in a pen measuring 1.9×5.8 m, allowing ca.
200 1.0–1.1 m^2 per pig. Pens had a solid floor which was covered with approximately 5 kg of
201 long straw. Pens were cleaned daily and provided with ca. 3.5 kg of fresh straw. Pigs had ad
202 libitum access to water and pelleted commercial feed.

203

204 *Habituation*

205 To reduce the possibility of fear responses in the test situation, pigs were habituated to the
206 study by being gradually exposed (over six occasions) to being alone for a few minutes and to
207 being handled in a weigh crate.

208

209 *Testing for aggressiveness*

210 Aggressiveness as a personality trait was the main factor under investigation in this study,
211 and the contests were based on differences in aggressiveness. Aggressiveness was estimated
212 by the resident-intruder (RI) test at 9 weeks of age. The RI test is an established test in
213 behavioural research that is undertaken to obtain a quantifiable measure of individual
214 aggressiveness (Koolhaas et al., 2013). In pigs the RI test has been shown to be consistent
215 over time (D'Eath, 2004) and to be predictive of aggressiveness when animals are mixed with
216 multiple unfamiliar animals (Erhard et al., 1997). In the test a 'resident' was kept individually

in a separate part of its home pen. Immediately after, an inferior 'intruder' was put into the home pen of the resident, in this case a pig weighing ca. 65% of the body weight of the resident. This created a situation in which the resident was likely to attack the inferior intruder. The latency until one of the animals attacked with a rapid sequence of bites was recorded. If the resident did not attack within 5 min after initial contact the test was ended and the latency was set at 300 s. The test was repeated the following day with a different intruder. The Pearson correlation between the attack latency of both test days was 0.58 (df = 102, $P < 0.0001$). The attack latencies of both days were summed to obtain a single variable for aggressiveness. This resulted in attack latencies that could take a value between 0 and 600, with 0 being highly aggressive and 600 being unaggressive.

Contests

Contests were staged between pairs of pigs at 10 weeks of age. Dyads were matched for body weight (on average 3.6 ± 0.3% difference), a traditional and validated measure of RHP in pigs (Andersen, Andenæs, Bøe, Jensen, & Bakken, 2000; Jensen & Yngvesson, 1998; Rushen, 1987), and differed in aggressiveness as reflected in the attack latency of the RI test. Dyads were formed between animals from opposite sides of the distribution of attack latency (high against low, N = 16), or from pigs at one tail of the distribution matched against animals with an average attack latency (high against intermediate, N = 19, and low against intermediate, N = 17). Both sexes were matched randomly as existing literature is ambiguous and does not give a consistent indication of sex differences for young pigs regarding agonistic behaviour (Clark & D'Eath, 2013; Jensen & Yngvesson, 1998; Rushen, 1987). Excluding sex also facilitated the creation of dyad combinations based on the factors of interest to the

research question, namely body weight and aggressiveness. Sex differences were accounted for in the statistical models.

The contest arena measured 2.9×3.8 m and had a light bedding of wood shavings covering the solid floor. The two animals entered the contest arena simultaneously from opposite sides. The time was started from the moment both had entered the arena. A single observer recorded the time until the first nose-to-nose contact, the first bite and the first fight, as well as the duration of display behaviour, pushing and fighting, and the frequency of unilateral bites (see ethogram, Table 1). Timing was stopped when a clear winner was apparent, which was when one pig retreated after being attacked and failed to retaliate within 2 min after retreat. The outcome was recorded as undecided if no winner was apparent within 30 min, after which the test was ended, or if a test had to be ended because of repeated escape attempts by one or both of the animals. 'Contest' duration refers to the total time that the opponents were in the contest arena, from entering the arena until a winner was apparent. The 'fight' duration refers to escalated reciprocal aggression (see ethogram, Table 1). Only contests with an outcome (winner/loser) were retained in the data, which excluded five contests (four were ended due to a fear response or mounting; one contest reached the maximum time without fighting). This resulted in 52 contests (104 pigs, 55 males and 49 females).

Physiological parameters

Immediately pre- and postcontest a few drops of blood were obtained from the ear vein by pricking it using a capillary blood lancet with a flat blade. The blood drops were directly applied to the test strips of a blood glucose meter (Accu-Chek, Aviva Blood Glucose System) and blood lactate meter (The EDGE Lactate Analyser) developed for humans. Pig blood is comparable to human blood (Marascalco, Ritchie, Snyder, & Kameneva, 2006; Weng,

Cloutier, Pibarot, & Durand, 1996), and therefore the meters developed for humans were regarded as more suitable than ones available for companion animals. The lactate meter had a test range of 0.7–22.2 mmol/litre. In seven cases the upper threshold was reached after fighting and these values were set to 22.2. Sampling order was randomized for the level of aggressiveness and contest outcome. A proportional increase was calculated as the post-test value divided by the pretest value. Owing to practical and technical errors two pretest samples for lactate and glucose, four post-test lactate samples and six post-test glucose samples could not be obtained. This resulted in four missing values for the proportional increase in blood lactate and six missing values for the increase in blood glucose.

Statistical analysis

Data were analysed with SAS 9.3 (SAS Inc., Chicago, IL, U.S.A.). Contest data were analysed as described in Briffa et al. (2013), while also including batch and litter as random effects which are important to account for. To test for evidence of assessment of aggressiveness (either self- or mutual assessment), the models detailed below use an appropriate statistical framework (as advocated by Taylor & Elwood, 2003, and reviewed in detail by Arnott & Elwood, 2009a), including winner and loser attack latencies (as our candidate RHP measure of aggressiveness), as well as the difference in attack latency between contestants. Self-assessment of aggressiveness would be indicated by a negative relationship between loser attack latency and contest duration (indicating that more aggressive losers fought for longer), with no significant relationship between winner attack latency and contest duration, nor any relationship between difference in attack latency between contestants and contest duration. With mutual assessment of aggressiveness there would also be a negative relationship between loser attack latency and contest duration but a significant positive relationship between winner attack latency and contest duration

(indicating that if losers assess their opponent to be highly aggressive, they give up quickly), and a negative relationship between difference in attack latency and contest duration.

Continuous data (attack latency, durations and frequency of biting) were checked for normality of the residuals and were transformed if required to obtain a normal distribution. First, a mixed model was applied to test whether sex, weight and litter had an effect on the attack latency in the RI test, whereby batch was the only random effect in the model statement. Thereafter, normally distributed data were analysed using a mixed model (PROC MIXED) and binary data (e.g. contest outcome) were analysed with a generalized linear mixed model (PROC GLIMMIX) with a binary distribution and logit link function. All models included outcome status as a repeated statement, with the contest as the experimental unit, to account for nonindependence between opponents (Briffa & Elwood, 2010). Batch and litter were included as random effects. The models initially included all relevant explanatory variables and interactions and these were then stepwise removed from the model if the significance level was above 0.10. The explanatory variables were body weight, aggressiveness (in attack latency), sex and the proportional increase in blood lactate and glucose (which were both unaffected by body weight). To assess these variables for both winners and losers the interaction outcome*treatment was assessed (Briffa & Elwood, 2010), with treatment referring to the explanatory variables body weight, attack latency, sex, lactate and glucose. Although dyads were matched for equal body weight we did include the (absolute and relative) difference in weight between the opponents to investigate whether this affected the outcome of the contest. Data are presented as means with SEs, and covariance parameter estimates are obtained by REML (default in SAS).

RESULTS

313 *Aggressiveness as a personality trait*

314 The attack latency in the RI test provided a very accurate reflection of individual
315 aggressiveness during the contest. Pigs with a short attack latency, which were regarded as
316 more aggressive, had a higher probability of initiating the first nose-to-nose contact ($F_{1,82}$ =
317 6.5, P = 0.01), the first bite ($F_{1,85}$ = 14.1, P <0.001) and the first fight ($F_{1,86}$ = 9.3, P = 0.004)
318 than pigs with a long attack latency in the RI test (Fig. 1). Females had a shorter attack
319 latency than males, meaning they were slightly more aggressive in the RI test (males: 293 ±
320 24 s; females: 210 ± 25 s; $F_{1,83}$ = 5.6, P = 0.02). The attack latency tended to be unrelated to
321 body weight ($F_{1,83}$ = 2.7, P = 0.10) and differed significantly between litter groups ($F_{16,83}$ =
322 2.1, P = 0.02).

323

324 *Contest duration*

325 The total duration of the contest, from the moment that the contestants entered the arena until
326 a winner was apparent, was on average 5½ min (339 ± 19 s). Of this time, pigs spent on
327 average 87 ± 6 s on display behaviour, 35 ± 6 s on nondamaging but energetically demanding
328 mutual pushing and 54 ± 6 s on fighting. The individual aggressiveness of the winner and
329 loser (in attack latency) did not influence the contest duration, the duration of display or
330 pushing, or the duration of fighting (all P > 0.10). However, asymmetry in attack latency did
331 affect durations. The greater the difference in aggressiveness, i.e. attack latency, between the
332 opponents the longer the contest was (Fig. 2; b = 0.37 ± 0.1 s/s difference in attack latency;
333 $F_{1,79}$ = 4.5, P = 0.04). Thus, contests between a highly aggressive opponent and one showing
334 little aggression took longest to reach an outcome. This was also apparent for the duration of
335 the display phase (b = 0.13 ± 0.0 s/s difference; $F_{1,84}$ = 9.6, P = 0.003) and the duration of
336 mutual pushing (b = 0.11 ± 0.0 s/s difference; $F_{1,79}$ = 5.8, P = 0.02), but not for the fight

337 phase ($F_{1,58}$ = 1.4, P = 0.24). Analysis of biting behaviour revealed that the more aggressive
338 contestant within a dyad bit the opponent more frequently (bites/min; excluding bites during
339 mutual fights) when asymmetry was greater whereas the less aggressive animal did not alter
340 its biting behaviour when the opponent was relatively more aggressive (Fig. 3; $F_{2,85}$ = 6.8, P
341 = 0.002). The duration of the total contest, the display phase and the pushing phase was
342 longest when the two opponents were males and shortest when they were females (Table 2).
343 The duration of the contest, as well as the duration of the separate phases, was unaffected by
344 winner and loser body weight (all P > 0.10), but heavier dyads escalated more often to the
345 fighting phase than lighter dyads (fight did not occur: 33 ± 2 kg; fight occurred: 35 ± 2 kg;
346 $F_{1,83}$ = 5.9, P = 0.02).

347

348 *Contest outcome*

349 Aggressiveness during the RI test, reflected in attack latency, was unrelated to the contest
350 outcome, with the attack latency of the losers being 264 ± 25 s and the attack latency of the
351 winners being 249 ± 24 s ($F_{1,86}$ = 0, P = 0.99). The outcome of the contests between weight-
352 matched pigs was most related to which animal initiated the first bite ($F_{1,83}$ = 10.6, P <
353 0.002). In 65% of all contests the pig that initiated the first bite won the contest. However, as
354 shown above, the first bite was almost always initiated by the more aggressive opponent. As
355 illustrated in Fig. 4, the relationship between aggressiveness and winning is obscured by the
356 occurrence of a fight. If the recipient of the first bite retaliated and the contest proceeded into
357 a fighting phase, then aggressiveness and bite initiation did not determine the outcome
358 between size-matched pigs. If, however, the recipient of the first bite did not retaliate or if
359 retaliation did not result in escalated fighting, then bite initiation was directly related to a high
360 likelihood of winning (in the 14 contests without a fight 13 were won by the opponent that

initiated the first bite). The next best predictor of contest outcome was the absolute weight difference between the opponents. Dyads were matched for equal weight but an average size difference of 3.6 ± 0.3% remained, with a maximum of 9.4%. Despite the minimal weight differences the winners were on average 0.5 ± 0.3 kg heavier than the losers ($F_{1,83}$ = 9.7, P = 0.002). All other variables were unrelated to the contest outcome (P > 0.10).

Physiological costs

Prior to the contest the average blood lactate value measured 2.4 ± 0.1 mmol/litre (range 0.7–6.7) and blood glucose measured 6.1 ± 0.1 mmol/litre (4.3–8.5). After the contest lactate increased to 10.4 ± 0.7 mmol/litre (0.7–>22.2) and glucose to 7.4 ± 0.1 mmol/litre (5.0–11.1). From these values the proportional change was calculated and used for further analyses. Blood lactate, but not blood glucose, increased with the overall contest duration, whereby each minute blood lactate increased on average 45% compared to the precontest value ($F_{1,79}$ = 10.6, P = 0.002). During escalated fighting, blood lactate increased on average 402% per minute spent in this behaviour compared to the pretest value ($F_{1,52}$ = 9.1, P = 0.004), and blood glucose increased 21% per minute of fighting compared to the pretest value ($F_{1,52}$ = 14.9, P <0.001). The traditional measure of contest costs, namely contest duration, is typically plotted against RHP to study assessment strategies. Substituting contest duration with blood lactate revealed no relationship that could indicate an assessment strategy (there were no significant relationships between lactate and aggressiveness, difference in aggressiveness or body weight). The blood values prior to the contest as well as the proportional increase during the contest did not influence the contest outcome (all P > 0.10).

DISCUSSION

Aggressiveness as a component of RHP

Aggressiveness, assayed in terms of attack latency during a resident-intruder test, did not directly relate to the outcome of the contest, suggesting aggressiveness is not a component of RHP. This was contrary to our initial prediction that the more aggressive individual in a contest would be more likely to win. However, aggressiveness showed an indirect relationship with contest outcome via bite initiation in contests without an escalated fight. The more aggressive individuals almost always initiated the first bite, which validated our personality measure from the RI test. If the contest did not then proceed to an escalated fight, this bite initiation was an effective strategy for winning, which is in line with existing literature (e.g. Guderley & Couture, 2005). Rather than viewing aggressiveness as a component of RHP the aggressiveness displayed by an individual can also be viewed as a signal of intent (Laidre & Johnstone, 2013; Searcy & Nowicki, 2005). More aggressive pigs were more likely to initiate biting, which would reflect an honest signal of their intention to attack. However, the fact that aggressiveness was unrelated to outcome suggests it does not provide an honest signal of RHP. This is further supported by examining those contests that escalated to fighting, because in these cases bite initiation, and thus aggressiveness, did not affect the outcome. Thus, more aggressive pigs signal their intent to attack, but this does not disclose accurate information on their likelihood of winning. It has been debated whether honest signals of intent could be evolutionarily stable (e.g. Maynard Smith & Parker, 1976; Maynard Smith, 1979). The inclusion of handicap theory (proposing that high-quality individuals are better able to display costly signals than low-quality individuals; Zahavi, 1975) showed that honest signalling was probable (e.g. Enquist, 1985; Grafen, 1990). More

recent models show that honest and deceitful signals can coexist in a stable system (Adams & Mesterton-Gibbons, 1995; Számadó, 2000).

Assessment of aggressiveness

We found no evidence that aggressiveness is assessed as part of either a self- or mutual assessment strategy. The correct statistical framework was used (Arnott & Elwood, 2009a; Taylor & Elwood, 2003), in which effects of winner and loser measures of RHP (aggressiveness expressed as attack latency) on contest cost were examined. Furthermore, we tested a number of measures of contest cost including duration and duration of separate phases, and we used blood lactate and blood glucose to provide measures of physiological costs. However, the results of this study should be interpreted with some caution as the sample size was limited (although comparable with other studies, e.g. 48 contests in Rudin & Briffa, 2012), and 27% of the dyads did not fight. The fact that some contests did not escalate is something that should be taken into account as it may comprise a substantial part of the sample size. For example, Stuart-Fox (2006) reported that in only 42 of 107 contests did both opponents escalate to biting and McGinley et al. (2015) reported that in only 34 of the 85 contests did the opponents come into contact. These high frequencies of nonescalated contests may point out that conflict avoidance is an important strategy which deserves further research attention.

McGinley et al. (2015) recently questioned the validity of using total contest duration as a surrogate measure for contest cost. Results from this study add to those concerns. Blood lactate, which is a more direct measure of cost, increased almost 10-fold more per minute of fighting than per minute of total contest duration. In the present study, contest duration comprised the time from entering the contest arena until a clear winner was apparent. In

between agonistic interactions, and before an outcome was reached, opponents could spend a considerable amount of time in activities unrelated to conflict and also using low-cost display behaviour. The duration of escalated fighting and phases of physical contact (e.g. pushing) may therefore provide better measures of cost than the overall contest duration, as may measuring the intensity of a contest.

That aggressiveness (in terms of attack latency) did not seem to form part of the information-gathering process used by pigs is perhaps unsurprising for a number of reasons. First, assessing aggressiveness might be highly cognitively demanding. It implies an awareness of one's own consistency in behaviour (Held, Mendl, Laughlin, & Byrne, 2002; Mendl & Paul, 2004). Self-knowledge of one's own morphological traits, which generally remain the same over a sustained period of time, may naturally occur through movement and executing strength and does not have to be cognitively demanding (Fawcett & Mowles, 2013). Self-knowledge of aggressiveness, however, would require memory of one's past behaviour, and possibly the consistency thereof over time, and subsequently using that information in an encounter. In terms of mutual assessment, assessing the aggressiveness of oneself as well as that of an opponent would seem like a rather difficult task. Erhard et al. (1997) suggested that pigs may be capable of assessing aggressiveness. When we investigated this using the recommended framework, there was no evidence that aggressiveness is assessed. Second, given that there was no effect of aggressiveness on contest outcome, it would not provide a reliable RHP cue for assessment, with alternative morphological traits such as body weight providing much better candidates for assessment. Indeed, there was some support for this. Although pigs were matched for body weight, the small difference that existed was sufficient for heavier individuals to be more likely to win. Body weight is therefore further validated as an RHP trait. Moreover, although not the focus of this study, the finding that heavier dyads were more likely to escalate the contest to fighting than lighter dyads is suggestive of self-

assessment. The assessment abilities of pigs in relation to traditional RHP measures (body weight and size) are currently the focus of study by our research group.

Asymmetry in aggressiveness between opponents

When RHP is reflected in body size, a greater asymmetry between the opponents is expected to decrease the contest cost and duration (e.g. Taylor & Elwood, 2003). We found that when the asymmetry in aggressiveness increased the contrary occurred, whereby the contest duration and the duration of display and mutual pushing increased, while the fight duration remained unaffected. A greater asymmetry in RHP traits is assumed to facilitate the assessment of fighting ability and would thus sooner result in withdrawal of the inferior individual (Arnott & Elwood, 2009a; pigs: Andersen et al., 2000), and may avoid escalated fighting. Irrespective of assessment of aggressiveness, the behavioural interactions within a contest might explain this discrepancy. The difference in unilateral biting behaviour suggests that pigs showing little aggression attempt to avoid a conflict by refraining from biting the opponent. More aggressive pigs bite, regardless of the contest duration, more often than less aggressive pigs when the asymmetry in aggressiveness is large (Fig. 3). This may be a logical response to the level of challenge. When both opponents retaliate equally to each other's attacks, the intensity of the contest may rapidly increase and contestants may sooner move towards escalated aggression (Maynard Smith & Price, 1973). If one opponent avoids confrontation but does not signal a clear retreat the contest may be prolonged until eventually one gives up, either with or without escalated aggression prior to the withdrawal. As opponents were expected to be physically similar in strength, the fighting phase itself seemed to unfold irrespective of absolute aggressiveness or the asymmetry in aggressiveness between the opponents.

Integrating personality with contest theory

More aggressive animals were more likely to initiate a bite whereas they were not more likely to win when they did so. This is similar to the findings of Bolhuis, Schouten, Schrama, and Wiegant (2005) that proactive pigs initiated more fights but did not acquire higher social ranks. As outlined above, this could be seen as a dishonest or unreliable signal of fighting ability whereas it is an honest signal of intent (Adams & Mesterton-Gibbons, 1995; Laidre & Johnstone, 2013; Számadó, 2000). It may have been that these animals were more willing to engage in aggression (Hofmann & Schildberger, 2001), which would be in line with the measure of aggressiveness from the RI test. It could also be that they initially overestimated their RHP compared to that of the opponent. If this is true, it is unlikely to result from being a large pig in a litter of smaller siblings as body weight compared to littermates did not affect bite initiation (results not shown). Overall, the behaviour shown by the pigs with a more aggressive personality is in line with previous studies showing that animals with a proactive coping style, which reflects personality, are more aggressive, rigid and impulsive in their behaviour (Koolhaas et al., 1999; pigs: Bolhuis et al., 2005; Melotti, Oostindjer, Bolhuis, Held, & Mendl, 2011). A personality trait has been defined as 'a specific aspect of a behavioural repertoire that can be quantified and that shows between-individual variation and within-individual consistency' (Carter, Feeney, Marshall, Cowlishaw, & Heinsohn, 2013, p. 467). As such, the attack latency in the RI test showed considerable variation between individuals and a moderate correlation within individuals. This repeatability adds to the existing studies that indicate that the RI test reflects aggressiveness as a personality trait (Carere, Drent, Privitera, Koolhaas, & Groothuis, 2005; D'Eath, 2004). The evidence for a link between animal personality and contest behaviour has recently been reviewed (Briffa et al., 2015). However, the majority of studies in this area have focused on investigating links

along the bold–shy personality spectrum, and proactive–reactive behavioural syndrome, and contest behaviour (Briffa et al., 2015: Table 1, out of 16 cited studies only one investigated links between aggression directly and RHP). The limited research that has been conducted on aggressiveness in relation to contest behaviour has produced conflicting results (McEvoy et al., 2013; Wilson et al., 2013; see above). Our study adds another layer of complexity by the findings of an indirect effect of aggressiveness on contest behaviour (bite initiation). While this may provide an honest signal of intent, it did not form a component of RHP, revealed by a lack of effect on contest outcome. Animal personality is a broad concept and attributed personality types often depend strongly on the tests that are chosen to reflect the personality type and the subsequent interpretation of the test results (Carter et al., 2013). Studying aggressiveness specifically as a component of personality, rather than personality as a whole, enables a closer understanding of how aggressive behaviour specifically may affect contest decisions, and may aid in the understanding of contest behaviour.

Sex differences

The literature is ambiguous about sex differences for aggressiveness and contest behaviour in pigs (Clark & D'Eath, 2013; Jensen & Yngvesson, 1998; Rushen, 1987). We therefore randomly staged contests with regard to sex. Male dyads had the longest contest duration and spent most time in display and mutual pushing. Intersexual differences in contests have been acknowledged in various species and might be due to energy reserves and hormonal state (Briffa & Sneddon, 2007), as well as different selection pressures acting on each sex (Arnott & Elwood, 2009b). The duration of escalated fighting did not differ between the sexes, which implies that males and females fight up to their maximum capacity and are at this age similar

529 in strength or persistency. We recommend that sex differences are considered in the study of
530 aggressiveness, including when pigs are prepubertal.

531

532 *Lactate and glucose*

533 The levels of blood lactate increased linearly with the contest duration and fight duration,
534 consistent with existing literature (Briffa & Sneddon, 2007). There were no differences
535 between the winner and loser for either the precontest value of blood lactate and glucose or
536 the proportional increase during the contest. Previous studies showed that losers have higher
537 blood lactate (e.g. Neat, Taylor, & Huntingford, 1998b; Schuett & Grober, 2000) and lower
538 glucose values than winners (Briffa & Elwood, 2005). The absence of a winner–loser effect
539 for metabolic costs suggests that losers retreated for reasons other than energetic constraints.
540 Pig blood is comparable to that of humans (Marascalco et al., 2006; Weng et al., 1996), and
541 in humans blood lactate has been studied in relation to exercise and sport competitions
542 (reviewed by Billat, 1996). Blood lactate measured during the contests was comparable to
543 values reported in human sport physiology (Billat, 1996). Some fights resulted in extreme
544 values, around 20 mmol/litre, which compare to short-lived intense peak performances in
545 human sport competitions (Billat, 1996; Vescovi, Falenchuk, & Wells, 2011). In commercial
546 pig production, the energetic costs of aggression are typically ignored by farmers. The lactate
547 values observed in this study, in which aggressive interactions were limited to a maximum of
548 30 min in contrast to commercial practice in which aggressive interactions continue over a
549 sustained period of time, emphasize that fights are extremely energetically demanding and
550 should not be overlooked.

551

Conclusion

Aggressiveness as a personality trait had no effect on the outcome of the contest, suggesting it does not form an important component of RHP in pigs. However, it did influence contest behaviour, in terms of bite initiation, and the fact that bite initiation was related to contest outcome could be interpreted as an indirect effect of aggressiveness on contest outcome. This personality trait could also act as an honest signal of intent. However, despite providing a source of potentially useful honest information regarding behavioural consistency that would be predictive of future behaviour, there was no evidence that pigs assessed aggressiveness. The appropriate theoretical approach comparing different models of assessment was used to reach this conclusion.

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792

Tables

Table 1. Ethogram

Behaviour	Description
Nose-to-nose	Nose approaches within 5 cm of the snout of the other
Display	Parallel walking (move simultaneously with the shoulders next to each other); heads up (both have their nose lifted high up in the air alongside each other); shoulder-to-shoulder (standing or moving with the shoulder against the shoulder of the other without real pressure)
Mutual pushing	Head or shoulder is used to move the other aside by applying pressure
Unilateral bite	Opens mouth and delivers a bite that contacts the other
Mutual fight	Rapid sequence of bites which are retaliated with a similar aggressive act from the opponent within 5 s
Withdrawal	Turns its head away from the opponent and retreats from further attacks by not showing any aggressive behaviour within 10 s

799 **Table 2.** Duration (s) of the total contest and its separate phases (*N* = 52) for the different

800 combinations of sexes in a dyad

Duration	MM	MF	FF	*P*
Contest	366 ± 27^{b}	$363 \pm 35^{a,b}$	266 ± 25^{a}	0.07
Display	112 ± 11^{b}	86 ± 8^{b}	56 ± 6^{a}	<0.001
Pushing	65 ± 15^{b}	26 ± 8^{b}	16 ± 8^{a}	<0.001
Fighting	50 ± 6^{a}	57 ± 9^{a}	57 ± 16^{a}	0.58

801 Dyads are male–male (MM, *N* = 15), male–female (MF, *N* = 25) and female–female (FF, *N* =

802 12). Values are back-transformed means with SEs. *P* values indicate the significance of the

803 overall effect of sex on duration. Fight duration is given only for the contests with a fight (*N*

804 = 38: 11 MM, 18 FM, 9 FF). Values lacking a common letter differ by $P < 0.05$.

805

Figure captions

Figure 1. Probability of initiating behaviour in a contest depending on the aggressiveness of a pig as reflected in the attack latency in the RI test. The lines show the probability of initiating the first nose-to-nose contact, the first bite and the first fight. Note that a low value for attack latency indicates high aggressiveness and a high value indicates low aggressiveness.

Figure 2. The relationship between the contest duration and the absolute difference in attack latency between the opponents as measured in the RI test, which reflects aggressiveness.

Figure 3. The effect of asymmetry in aggressiveness, shown in the difference in attack latency from the RI test, on the rate of unilateral biting per minute (separate from fights) for the most aggressive opponent (circles and solid line) and the least aggressive opponent (crosses and dashed line).

Figure 4. Values depict the average attack latency (AL; s) for contestants that did or did not initiate the first bite in a contest that either did or did not include a fight, with the number of winners and losers per outcome.